

PERSISTENCE OF ^{14}C LABELED CARBON IN *LARREA TRIDENTATA* UP TO 40 MONTHS AFTER PHOTOSYNTHETIC FIXATION IN THE NORTHERN MOJAVE DESERT

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ABSTRACT.—*Larrea tridentata* (Sesse Moc. ex DC) Cov. exposed to $^{14}\text{CO}_2$ retained about 20 percent of its ^{14}C after 16 and also after 26 months. In leaves, however, a lower specific activity was present at 26 months than at 16 months, and a smaller percentage of ^{14}C in the plant occurred in leaves at 26 months than at 16 months (3 percent vs. 10 percent). This indicates some, but little, reuse of carbon from the structural components of the plants. The strong tendency of the species to retain this carbon may be related to a survival mechanism. After 40 months the results were more erratic, with 11 percent of the ^{14}C remaining in plants and only 2 percent of the total remaining in the leaves. The specific activity of ^{14}C in the organic debris fraction obtained with saturated salt flotation of roots after small and fine roots had been physically removed indicated that from 27 to 35 percent of the organic debris had the same specific activity as roots and probably could be considered as roots. This compares with the 45 percent value determined previously by a different technique. The below-ground to aboveground ratio for biomass of these plants was about 2.5:1. The below-ground to above-ground ratio for the ^{14}C was about 0.5 at 16 months, 1.3 at 26 months, and 2.5 at 40 months. The estimates obtained in this study were used to correct our previous data for below-ground biomass. Accordingly, somewhere between 3000 and 5000 kg/ha roots are present in the Rock Valley area. An increase with time of the below-ground to aboveground ^{14}C ratio probably indicates loss of ^{14}C from above-ground parts rather than additional transport to roots.

One difficult aspect of plant studies in deserts is that of estimating below-ground biomass. Our previous studies have emphasized the magnitude of this problem (Bamberg et al. 1973, 1974, Vollmer et al. 1975, 1976, and Wallace, Bamberg, and Cha 1974), and it is further emphasized by the wide differences in below-ground biomass reported for the same area by different workers within our own group using different techniques of measurement.

Some approximations for root:shoot ratios in our studies for the northern Mojave Desert are near 1:1, but others approach 4:1. In the Great Basin Desert root:shoot ratios were reported that varied from around 8:1 to more than 12:1 (Caldwell and Camp 1974, Caldwell et al. 1974, Caldwell et al. 1976). The purpose of this study was to determine the persistence of ^{14}C labeled carbon in *Larrea tridentata* (Sesse & Moc. ex DC) Cov. and to further assess the problem of root biomass of this desert species.

MATERIALS AND METHODS

Plants in Mercury Valley, Nevada, were exposed to $^{14}\text{CO}_2$ with techniques previously used (Bamberg et al. 1973, 1974, Wallace et al. 1974). Six naturally growing *L. tridentata* were exposed to $^{14}\text{CO}_2$ for 2 h on the morning of 14 May 1974. Each plant was exposed to 125 uCi $^{14}\text{CO}_2$. Twigs were sampled at the end of this 2-h period for use in estimating the total $^{14}\text{CO}_2$ fixed by the plants. Two of these plants were excavated 16 months later on 17 September 1975 (Vollmer et al. 1975). Samples of all parts were then counted for ^{14}C by Q-gas technique and corrected for self absorption by methods reported previously (Bamberg et al. 1973). Two other plants were excavated on 16 July 1976, and the last two plants were excavated for analysis on 21 September 1977.

Soil from within a radius of 2.5 times the radius of the plant canopy was sampled for use in fine root biomass determinations. Soil

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samples (1 liter) were added to a saturated NaCl solution. Soil organic matter was separated by flotation and hand-sorted to obtain fine roots. The organic debris which could not be identified as roots was also separated. These samples were prepared and counted for ^{14}C . The roots were dried and ashed and found to contain 60–75 percent non-combustible ash. The high ash content was due to soil and salt contaminants adhering to roots. Root weights were normalized to 25 percent ash. The amount of roots in the soil surrounding the plants was estimated by extrapolating from small soil samples to the total volume of soils within a radius of 2.5 times the radius of the plant canopy to a depth of 30 cm. This method is similar to that employed by Bamberg et al. (1974) and Vollmer et al. (1975).

RESULTS AND DISCUSSION

Larrea tridentata that had been exposed to $^{14}\text{CO}_2$ 16 months previously at the Nevada Test Site retained about 20 percent of the ^{14}C that was originally fixed (Table 1). This amount was essentially unchanged at 26

months (Table 2). At 26 months, however, a lower specific activity was found in leaves than at 16 months, and a smaller percentage of the remaining ^{14}C was in the leaves at 26 months (3 percent) compared with 16 months (about 10 percent). This is indicative of low respiratory turnover and low remobilization of carbon from the structural components of this desert shrub.

Even though *L. tridentata* is evergreen, it does have turnover of leaves close to annually (Wallace and Romney 1972), so there would be a regular loss of ^{14}C in an experiment such as this. The loss would not be as great as the ^{14}C content of leaves, however, because of the retranslocation of around 50 percent of the carbon from the leaves to the shrub before leaf abscission. Except for leaves, we were unable to distinguish between the ^{14}C contents of the two sets of plants collected at 16 months and at 26 months. Because three annual phenological cycles are involved for the pair of plants harvested at 26 months and because somewhere around 20 percent of the original fixed ^{14}C was still in the plants similar to that at 16 months, a survival mechanism may be in-

TABLE 1. Plant biomass and ^{14}C content within a radius of 2.5 times the canopy radius on 17 September 1975 for two previously tagged (16 months) *Larrea tridentata*.

	Plant No. 1		Plant No. 4	
	Grams	Biomass (dry weight) Percent	Grams	Percent
Leaves	30.3	8	38.2	8
Stems	118.5	20	90.9	19
Small roots (<1 mm)	52.1	—	80.1	—
Medium roots (1 to 3 mm)	109.0	—	164.0	—
Other roots	43.4	—	52.4	—
Total roots	204.5	52	296.5	61
Total roots*	245.4	62	355.8	73
Total	394.2	100	434.9	100

	Plant No. 1		Plant No. 4		
	cpm	Percent	cpm/g dry wt	cpm	Percent
May 1974	1,583,000	—	—	3,200,000	—
September 1976, total plant	283,300	100	751	481,700	100
Leaves	23,100	8	762	72,100	15
Stems	150,500	53	1270	211,400	44
Roots	91,500	32	447	165,100	34
Total roots corrected for organic debris*	109,700	39	447	198,200	41

*Organic debris corrected to specific activity of roots. See Table 2.

volved. A high degree of conservation of carbon occurred.

The third pair of plants originally exposed to $^{14}\text{CO}_2$ in May of 1974 was sampled at approximately 40 months. Data are in Table 3. About 2 percent of the remaining ^{14}C was in leaves at this date. About 11 percent of the original ^{14}C fixed remained in the plants.

The information in Tables 1 to 3 has bearing on the below-ground to aboveground ratio of biomass and the below-ground annual productivity of shrubs. Workers from the Great Basin desert have found larger proportions of roots than we have for the Mojave Desert (Caldwell and Camp 1974, Caldwell et al. 1974, Caldwell et al. 1976). Our original estimate of below-ground to aboveground ratios were low (around 1) (Wallace, Bamberg, and Cha 1974). More recent estimates for the Mojave Desert were around 2 or 3 (Vollmer et al. 1976, Bamberg et al. 1974).

The biomass root/stem ratios for the two

plants in Table 2 were 4.9 and 3.1; for ^{14}C the ratios were 1.9 and 1.1, respectively. The same values for the plant in Table 1 (16 months after labeling) were 2.1 and 3.9 for biomass and 0.7 and 0.9 for ^{14}C . The biomass root/stem ratios for the two plants sampled at 40 months were 6.0 and 7.6, and the ^{14}C ratios were 1.6 and 5.1. It appeared that the biomass ratio was slightly higher at 26 or 40 months than at 16 months and that the ^{14}C ratio generally increased as time passed by. Part of the difference, however, could be due to technique, and part may be due to loss of ^{14}C from aboveground parts with age.

The data in Table 2 further resolve the problem of whether or not organic debris floated from the soil samples with saturated solutions of salts should be considered as roots. Three factors relate to the problem. Such material is very high in ash because of the saturated salt and the soil contamination. Correction values are necessary. Not all sub-

TABLE 2. Plant biomass and ^{14}C content within a radius of 2.5 times the canopy radius on 16 July 1976 of two *Larrea tridentata* plants exposed to $^{14}\text{CO}_2$ 26 months previously at Mercury, Nevada (roots normalized to 25 percent ash).

	Plant No. 2		Plant No. 6	
	Grams	Biomass (dry weight) Percent	Grams	Percent
Flowers	5.5	1.0	5.1	0.8
Leaves	37.7	6.7	49.8	8.0
Stems	88.1	15.7	138.8	22.2
Roots	333.3	59.4	320.1	51.1
Organic debris ^a	355.8	—	275.9	—
Corrected value of O.D. ^{**}	96.7	17.2	111.8	17.9
Total roots	430.0	76.6	431.9	69.0
Total	561.3	100.0	625.6	100
Plant No. 2				
^{14}C Content				
	cpm	Percent	cpm/g dry wt	cpm/g dry wt
14 May 1974	2,793,000	—	—	—
16 July 1976, total plant	595,200	100.0	120	701,500
Flowers	665	0.1	110	510
Leaves	15,000	2.5	398	22,900
Stems	201,500	33.9	2,287	325,300
Roots	293,000	49.2	879	261,500
Organic debris ^a	85,000	—	239	91,300
Corrected value of O.D. ^{**}	85,000	14.3	879	91,300
Total roots	378,000	63.5	879	352,800
				563
				817

^aOrganic material floated from soil with concentrated NaCl + normalized to 25 percent ash. Some of it may be a very fine fraction of roots.

^{**}Organic debris corrected to specific activity of roots.

samples from soil about the ^{14}C -treated plants had ^{14}C in the organic debris floated from the soil samples, and such probably should not be considered as root material. In about 90 percent of the cases the fine roots contained ^{14}C , but only 10 percent of the organic debris samples contained the isotope. The specific activity of the ^{14}C in the organic debris is lower than that for roots (see Tables 1 and 2). Nonroot material then is involved to the extent of correction of weights to a constant specific activity as was done in Tables 1, 2, and 3. This, of course, could be erroneous because the ^{14}C could arise from dead, partially decayed roots. The proportion of the organic debris not considered as roots then was 73 percent and 60 percent for the two shrubs in Table 2. Vollmer et al. (1975) had determined that 45 percent of the organic debris was roots and the results of the two studies do not differ greatly.

The ratio of weight of roots to above-ground parts in Tables 2 and 3 varied from about 1.6 to over 3 with the corrected values

for roots. The average of all 4 cases was 2.5. The ratio of the root-shoot distribution of ^{14}C in the plants after the 26 months is also interesting (Table 1). The average ratio for the corrected root ^{14}C ratio was about 1.4. Neither the 2.5 nor the 1.4 ratio approach those found for Great Basin shrubs (Caldwell and Camp 1974). They do, however, indicate the presence of greater biomass below-ground than aboveground.

The root/stem ratio of 1.4 for ^{14}C from Table 2 is of further interest. After 26 months, more of the ^{14}C in the plants was below ground than above ground, which corresponds with the root weights. In our earlier studies (Wallace and Romney 1980, this volume) the ^{14}C ratio for root/stem was around 0.2 for the relatively short-time basis. The shift may be related to loss of ^{14}C -containing materials from shoots rather than to transport of more of it below ground. This would indicate that, over a period of years, there is a greater loss of aboveground parts than below-ground parts.

TABLE 3. Plant biomass and ^{14}C content within a radius of 2.5 times the canopy radius on 21 September 1976 of two *Larrea tridentata* plants exposed to $^{14}\text{CO}_2$ 40 months previously at Mercury, Nevada (roots normalized to 25 percent ash).

	Plant No. 3		Plant No. 5	
	Grams	Biomass (dry weight) Percent	Grams	Percent
Leaves	59.3	9.0	52.1	11.6
Stems	86.2	13.1	46.1	10.0
Roots	247.3	37.4	206.3	45.9
Organic debris ^a	864.7***	—	428.2	—
Corrected value of O.D. ^{**}	267.0	40.5	145.2	32.3
Total root	514.3***	77.9	351.5	78.2
Total	659.8	100.0	449.7	100.0

	Plant No. 3		Plant No. 5			
	cpm	Percent	cpm/g dry wt	cpm	Percent	
14 May 1974	3,049,000	—	—	5,985,000	—	—
21 Sept. 1977, total plant	220,300	100.0	333.9	825,600	100.0	—
Leaves	6,000	2.7	100.2	13,600	1.7	261.0
Stems	82,000	37.2	951.3	133,600	16.2	2898.0
Roots	63,600	28.9	257.5	506,600	61.4	2455.6
Organic debris ^a	68,700	—	79.5	171,800	—	832.7
Corrected value of O.D. ^{**}	68,700	31.2	257.5	171,800	20.8	2455.6
Total roots	132,300	60.1	257.5	678,400	82.2	2455.6

^aOrganic material floated from soil with concentrated NaCl + normalized to 25 percent ash. Some of it may be a very fine fraction of roots.

^{**}Organic debris corrected to specific activity of roots.

***Value is abnormally high because of a broken irrigation sprinkler nearby which resulted in much grass in the area.

In 1974, we made some estimates of root biomass for the northern Mojave Desert (Table 2 of Wallace et al. 1974). It would appear from the data reported here that the root values of the earlier study probably should be further corrected to include the root portion in the organic debris portion. An estimated correction factor is the corrected versus the uncorrected values in Table 1. These are 1.29 (430/333) and 1.35 (432-320) for weights of the two plants, and the values in Table 2 of Wallace et al. (1974) should be corrected by that amount (mean = 1.32). An interspace correction should also be made in that the 1974 samples were extended into the interspace soil only as far as we found roots. The development of a correction factor of 1.23 for interspace is given elsewhere, and the values for the earlier data are calculated in Table 4.

The twice-corrected values for root/stem in Table 4 is 1.73 and for root/root + stem is 0.63. These values are, of course, subject to errors, but they are still lower than comparable data from the Great Basin desert.

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TABLE 4. Estimates of standing stem and root weights for plot at Rock Valley (from a 0.46 km² plot). (Revised from Wallace et al. 1974.)

Species	No. of plants/ha	Calc. stem dry wt g/plant	Standard deviation of stem wt g/plant	Root		Root	
				Stem kg/ha	Root kg/ha	corrected for debris (1.32) kg/ha	corrected for interspace (1.23) kg/ha
<i>Acamptopappus shockleyi</i>	47	68.3	82.8	3.2	1.8	2.4	2.9
<i>Atriplex confertifolia</i>	75	33.7	32.8	2.5	1.1	1.5	1.8
<i>Ephedra nevadensis</i>	783	119.1	202.9	93.3	77.9	102.8	126.5
<i>Eurotia lanata</i>	478	62.7	96.9	30.0	27.0	35.0	43.8
<i>Aubrosia dumosa</i>	2394	108.7	111.0	260.2	301.0	397.3	488.7
<i>Grayia spinosa</i>	1196	74.3	85.8	88.9	64.0	84.5	103.9
<i>Krameria parvifolia</i>	1482	136.4	96.9	202.1	159.4	210.4	258.8
<i>Larrea tridentata</i>	1046	437.9	454.1	458.0	566.7	748.0	920.1
<i>Larrea andersonii</i>	710	171.2	244.3	263.7	220.1	290.5	357.4
<i>Lycium pallidum</i>	459	264.4	216.4	121.3	199.7	263.6	324.3
Total	8670	—	—	1523.3	1618.7	2136.6	2628.2